Tree size, microhabitat, and hydraulic traits (interactively) shape drought response in a temperate broadleaf forest

Ian McGregor, Ryan Helcoski, Norbert Kunert, Alan Tepley, Valentine Herrmann, Joseph Zailaa, Atticus Stovall, Neil Pederson, Lawren Sack, Krista Anderson-Teixeira

Abstract

Predicting forest responses to drought is an increasingly critical task under climate change effects. Part of the problem is due to the lack of studies analyzing the confluence of leaf hydraulic traits with biophysical parameters. In this study, we analyze the interaction between these two trait groups using forest census data from a 25.6-ha ForestGEO plot in Virginia (USA). Drought periods were defined by both Palmer Drought Severity Indices (PDSI) and their identification from tree-ring records for 12 species representing 97% of woody productivity. Each drought scenario (1964-66, 1977, 1999), along with the overall trend, was then tested against leaf hyraulic trait measurements and microhabitat biophysical data. Individual-level growth responses to the three individual droughts were stronger among taller trees in dominant canopy positions, those in wetter microsites, and for more drought-sensitive species as assessed by leaf traits (turgor loss at less negative leaf water potential, greater shrinkage with leaf dehydration), with substantial variation in the best predictor variables across given droughts. We conclude that when droughts occur, large dominant trees, drought-sensitive species, and individuals in wetter microhabitats are likely to be most strongly affected.

Introduction

Understanding how and why trees respond to drought is critical to predicting forest drought responses and climate change feedbacks. (1 paragraph on this- I have lots of content on this and will add later.)

[Understanding forest responses to drought requires increased functional understanding of the factors that confer individual-level vulnerability or resistance.] Forests are diverse in terms of tree sizes and functional traits, and it is known that trees varying in size and functional traits respond differently to drought (e.g., (Bennett et al., 2015); REFS). Therefore, in order to understand whole-forest response to drought, we need a functional understanding of how responses vary by tree size, microhabitat, and species. There are 3 fundamental questions that must be addressed:

First, what drives the observed tendency for large trees to suffer more during drought?
Bennett et al. (2015) showed that in forests globally, large trees suffer greater growth reductions during drought. However, this analysis quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed two major mechanisms (besides insects) for the observed greater drougth growth reductions of large trees: (1) inherently greater biophysical challenge of being tall; (2) greater exposure of the crowns of large trees. Counteracting these effects, (3) the larger root systems of larger trees may confer an advantage in terms of allowing greater access to water, but it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure.

Canopy trees have lower drought resistance because they are exposed to higher solar radiation, greater wind speeds, and lower humidity. Alternatively, the generally supressed status of subcanopy trees may be insufficient to override the benefits of their buffered environment during drought.

Second, how do species' traits - alone and in interaction with tree size - influence drought response? Analyzing drought responses on the species level does not fully explain mechanisms and is not feasible in diverse forests. The solution is a trait-based approach. Leaf hydraulic traits hold more promise than more commonly/traditionally-measured traits such as wood density and specific leaf area (SLA) (Medeiros et al. 2019).

Commonly measured traits including wood density (REFS), leaf mass per area (Abrams, 1990) (Guerfel et al., 2009), and ring porosity (Elliot et al. 2015, Friedrichs et al. 2009) have been linked to drought responses and likely correlated with drought resistance in this forest. However, we hypothesize that leaf hydraulic traits such as leaf area shrinkage upon dessication (PLA) and turgor loss point (TLP), which are emerging as potentially more informative traits but whose effect on drought resistance has never been tested (CONFIRM), will prove better predictors.

Moreover, there may be an interaction between traits and tree size. It is possible that the pattern observed by Bennett et al. (2015) could be caused by smaller trees being more drought resistant. Alternatively, larger trees may have more drought-resistant traits as adpatations to greater biophysical challenges.

Third, are responses similar or variable across individual drought years? Droughts are rarely explicitly defined in ecological studies (Slette et al., 2019), yet no two droughts are the same.

We need to understand the the factors confirming drought vulnerability or resistance not only for extreme droughts with dramatic impacts on tree growth and mortality, which tend to dominate the literature (Bennett et al., 2015) (REFS), but also for more modest but frequent droughts–e.g., those with historical return intervals on the order of a decade.

Here, we combine tree-ring records covering three droughts (1964-66, 1977, 1999), species functional and hydraulic trait measurments, and forest census data from a 25.6-ha ForestGEO plot in Virginia (USA) to test a series of hypotheses and associated specific predictions (Table 1) designed to yield functional understanding of how tree size, microenrivonment, and species' traits collectively shape drought responses. First, we focus on the role of tree size and its interaction with microenvironement. We confirm that, consistent with most forests globally (Bennett et al., 2015), larger-diameter trees have lower drought resistance in this forest, which is in an ecoregion represented by only one study in Bennett et al (2015) (H1.0). We then test hypotheses designed to disentangle the relative importance of tree height (H1.1), crown exposure (H1.2), and root water access, which should be greater for larger trees in dry but not perpetually wet microsites (H1.3). Second, we focus on the role of species' functional and hydraulic traits and their interaction with tree height. We hypothesize that drought resistance will follow predicted and observed patterns in relation to wood density, specific leaf area, and ring porosity (P2.1a-c), but that leaf hydraulic traits such as leaf area shrinkage upon dehydration and turgor loss point will prove better predictors (P2.1d-e). We then test whether these traits correlate with tree height (P2.2), potentially driving the observed tendency for taller trees to suffer more during drought (P2.3). Finally, we focused on variability among droughts, asking how community resistance varied across droughts (H3.1) and whether the factors confirming vulnerability or resistance varied across droughts (H3.2).

Let's put Table 1 here. We need to give the hypotheses/ predictions here. It seems counterintuitive to put the results right up front like that, but it actually tends to be a higher-impact style of writing, and recommended here.

Table 1. **Summary of hypotheses, predictions and results**

	Prediction
	H1.0. larger-diameter trees have lower drought resistance
	1.0. Drought resistance decreases with DBH
	H1.1. Drought resistance decreases with tree height.
	1.1a- Drought resistance decreases with height
	1.1b- Height is a better predictor of drought resistance than DBH
	H1.2. Drought resistance decreases with canopy exposure
	1.2a- Canopy position alone predicts drought resistance (dominant < co-dominant < intermediate < suppressed)
	1.2b- After accounting for height, canopy position predicts drought resistance (dominant < co-dominant < intermediate < suppressed)
	H1.3. Drought resistance is linked to rooting volume in drier microhabitats
	1.3- There is a negative interactive effect between tree height and topographic water index
	H2.1. Species traits predict drought resistance
	2.1a - wood density correlates positively to drought resistant
	2.1b - leaf mass area correlates positively to drought resistance
	2.1c - diffuse porous species are more sensitive than ring porous
	2.1d -leaf area shrinkage upon dessication (PLA) is negatively correlated with drought resistance
	2.1e - TLP correlates negatively with drought resistance
	H2.2. More drought-resistant traits associated to taller trees
	2.1a - community mean wood density correlates positively to height
	2.1b - community mean leaf mass per area correlates positively to height
	2.1c - community fraction of diffuse porous species decreases with height
	2.1d - community mean leaf area shrinkage upon dessication (PLA) is negatively correlated with height
	2.1e - community mean TLP correlates negatively with height
	H2.3. Size-dependent drought resistance is driven by functional traits
	2.3. Inclusion of traits in the statistical model eliminates effect of height
	H3.1. Responses varied by drought
	3.1. Drought year explained variation in drought resistance
	H3.2. Predictor variables varied across droughts.
	3.2a. Directions of responses to predictor variables is consistent
	3.2b. Set of predictor variables in best model varies across droughts

We count predictions as fully supported (or rejected) when the direction of response matches (or contradicts) the prediction. H2.3-H3.2 are based on if models containing species traits in H2.1 had dAIC>=2 relative to the appropriate null model or to any alternative multivariate model within 2 dAIC. Parentheses indicate that predictions were partially supported (or rejected). In other words, parentheses indicate when the direction of response matched (or contradicted) the prediction in some but not all models with dAIC<2 relative to the appropriate null model. With categorical variables such as crown position, a "(yes)" notation describes when the trend matched the prediction, but it wasn't significant A "(yes/no) or ("no/yes")" indicates tendencies in opposite directions in univariate tests versus the best full models, respectively. "(yes)

Methods

Study site Research was conducted at the 25.6 ha ForestGEO (Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78° 08'43.4"W) (Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level (Gonzalez-Akre et al., 2016) with a topographic relief of 65m (Bourg et al., 2013). Dominant species include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Data collection and preparation The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems >= 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH (described below), along with tree location in the plot to determine the topographic wetness index. Furthermore, we used data for all stems >= 10cm to analyze functional trait composition relative to tree height. *I added the last sentence–not sure if you've described that below yet. I don't think you need to note here which data we use, so long as*

that's described in the portions where you describe the analysis.

We analyzed tree-ring data from the twelve species contributing most to woody aboveground net primary productivity (ANPP), which together comprised 97% of study plot ANPP between 2008 and 2013 (Helcoski et al., 2019). Cores were obtained in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals of DBH >= 10cm (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with Helcoski et al. (2019): (ITRDB; GitHub/Zenodo). *is this a database? Yes. Ryan submitted the data but I don't think its posted yet. We should also cite GitHub/Zenodo here. I'll come back to that.*

Height measurements (n=# trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository. Measurement methods included manual (Stovall et al., 2018a, NEON), digital rangefinders (Anderson-Teixeira et al., 2015b), and automatic LiDAR (Stovall et al., 2018b). Rangefinders either used the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. The associated errors for using either method were acknowledged (Larjavaara and Muller-Landau, 2013). Species-specific height allometries were developed (Table S# - **ADD THIS TABLE TO SI**). For species that didn't have enough height measurements, heights were calculated from equations derived from all species in the study.

For each tree, we combined tree-ring records and allometric equations of height and bark thickness to retroactively calculate DBH and estimate height for the years 1950-2009. Prior DBH was estimated using the following equation, using 2008 as the earliest year for having reliable DBH measurements:

$$diamYEAR = dbh2008 - 2*(bark.depth2008) - 2*\Sigma(ring.widthYEAR : ring.width2008) + 2*(bark.depthYEAR)$$

Here, *ring.width* was measured from cores. Bark thickness was estimated from species-specific allometries based on the bark thickness data of (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to DBH (Table S#- **create table to give these equations in SI**) and then used these to estimate bark thickness based on DBH.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol from (Jennings et al., 1999), whereby positions were ranked as dominant, codominant, intermediate, or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree's position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. XX) and height change since *1959* indicated that change was likely slow. [**work on this– provide details?**]

Topographic wetness index (TWI) was calculated using the (Metcalfe et al., 2018) package in R.

Hydraulic traits were collected from SCBI and are summarized in Table 1. In August 2018, we collected leaf samples from three individuals of each species . . . (**Nobby's description of methods for the following (see word document**) 1. PLA 2. LMA 4. Wood density 5. TLP

Table 2. Species analyzed here, listed in descending order of ANPP_stem. n cores and DBH range represented, and species traits [*This replaces/combines the two remaining tables in this section. Suggested columns, with those to include only if they fit in parentheses: species, (stems >=10 cm per ha in plot), (ANPP_stem), n cores, DBH range of cores, (n cores in each crown position) species means for each trait]

\begin{table}[!h]

\caption{Overview of analyzed species, detailing DBH mean and range of cored trees, the number of cores represented by each crown position of each species, and mean hydraulic trait measurements. Units of measurements are in mm (DBH), % (PLA), g/m2 (LMA), MPa (TLP), and g/cm3 (WD).}
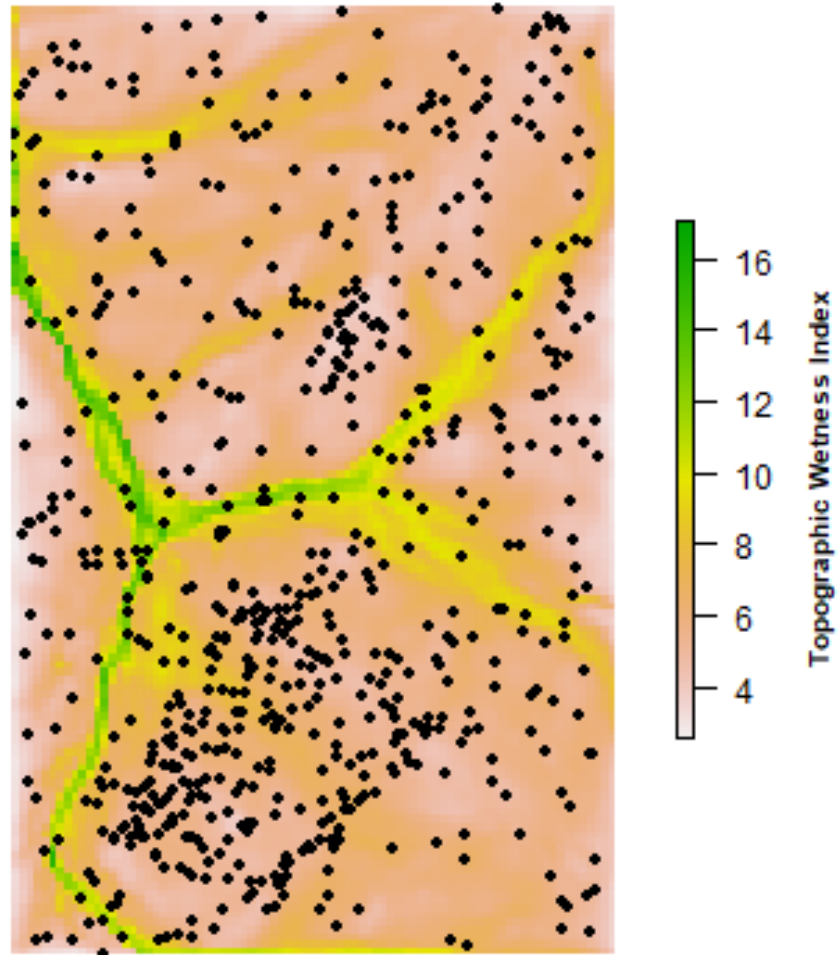
Figure 1: Location of cored trees

sp	mean_DBH	range_DBH	n_cores	dominant	co.dominant	intermediate	suppressed	prior.dead	RP
caco	271.87	508.0	13	NA	2	5	5	1	ring
cagl	313.89	887.0	31	1	8	16	5	1	ring
caovl	352.87	511.0	23	4	5	12	2	NA	ring
cato	209.74	201.1	13	NA	NA	6	2	5	ring
fagr	235.11	960.0	80	NA	7	48	25	NA	diffus
fram	353.63	883.3	62	NA	17	19	14	12	ring
juni	481.42	628.0	31	NA	21	8	NA	2	semi-
litu	368.54	904.0	98	9	29	25	30	5	diffus
qual	471.51	677.0	61	4	34	20	3	NA	ring
qupr	422.48	767.0	59	1	26	20	12	NA	ring
quru	548.79	1369.3	69	6	36	23	2	2	ring
quve	541.38	981.8	77	6	46	22	1	2	ring

\end{table}

Climate and drought years [**add description of climate data used in Fig. 1, NEON vertical profiles**]

To accurately understand climate sensitivity, this study used a specific definition of drought, which is not a common practice (Slette et al., 2019). We used the pointRes package (van der Maaten-Theunissen and van der Maaten, 2016) in R (version 3.5.3) to determine drought periods based on trees' drought resistance, which is defined by (Lloret et al., 2011) as the ratio between the performance during and before the disturbance. Candidate drought years were defined if >50% of the cored trees experienced <30% growth in a year compared to the previous 5 years. These were then cross-validated with the regional Palmer Drought Severity Index (PDSI) values for each year, which yielded a set of three periods that were consistently shown as drought: 1964-1966, 1977, and 1999.

Results

Once the data was collected, linear mixed models were run following the order of the hypotheses as seen in Figure ??? [individual_tested_traits]. Using the (van der Maaten-Theunissen and van der Maaten, 2016) package, we set up models with the resistance value as the response variable, and each prediction's variable as the independent variable. Variables' importance in predicting drought tolerance was calculated from mixed-effects models and the lowest AICc (Bates et al., 2019, Mazerolle and portions of code contributed by Dan Linden. (2019)).Null models were determined in order of the predictions. First, we analyzed the combined scenario to determine if "year" was significant. Upon establishing this, we tested height and DBH as size parameters. Although both were significant, height was kept due to its larger delta AICc compared with the null model. We then tested the remaining biophysical and hydraulic traits individually against a null model containing height and year. This yielded Figure ??? (cand_full). All variables with dAICc >2 were used as candidates for each scenario's best model (figure ???? (tested_traits_best))

Describe each individual drought scenario 1964-1966 1977 1999

Figure 1. Time series of peak growing season (May-August) climate conditions and residual chronologies for each species. Droughts analyzed here are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski et al., 2019).

Results for first main question: what drives the observed tendency for large trees to suffer more during drought? H1.0, H1.1, H1.2, H1.3 DBH, height, crown position, and TWI

Results for second main question: how do species' traits - alone and in interaction with tree size - influence drought response? H2.1, H2.2, H2.3 Hydraulic traits alone, traits with height
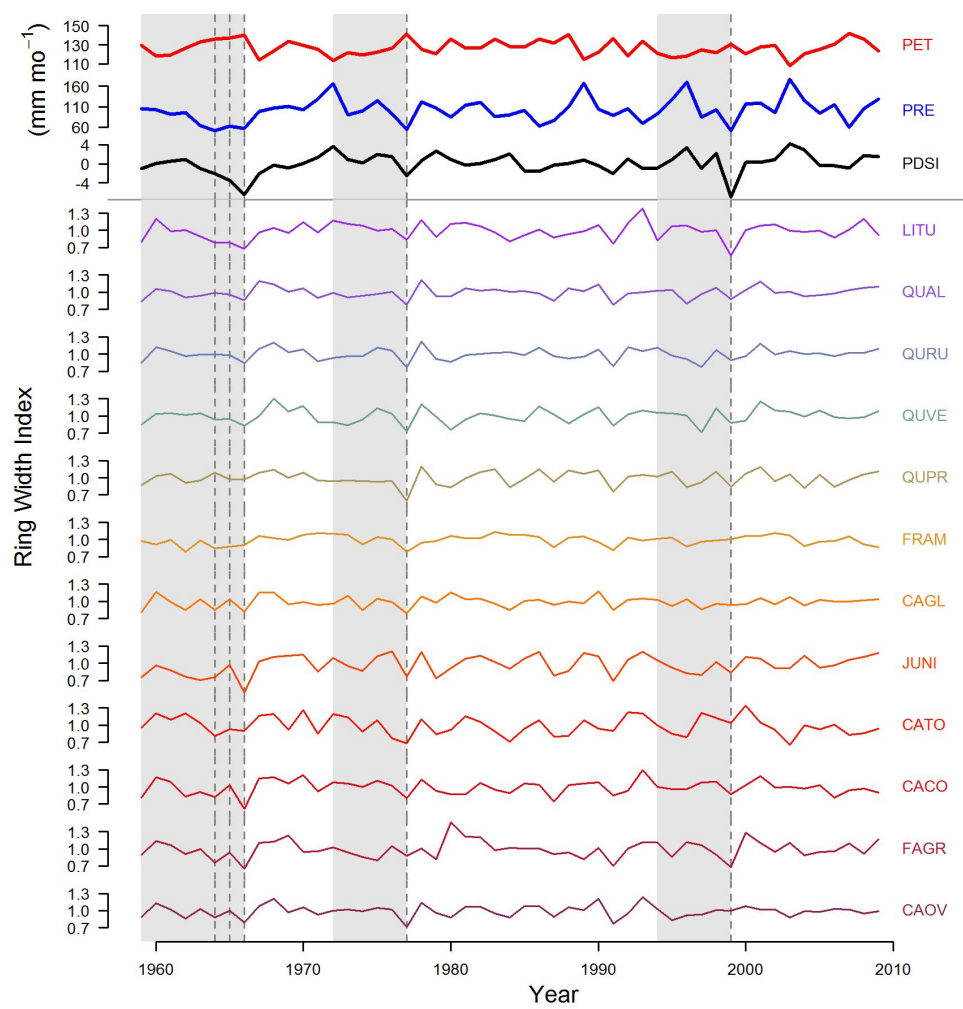
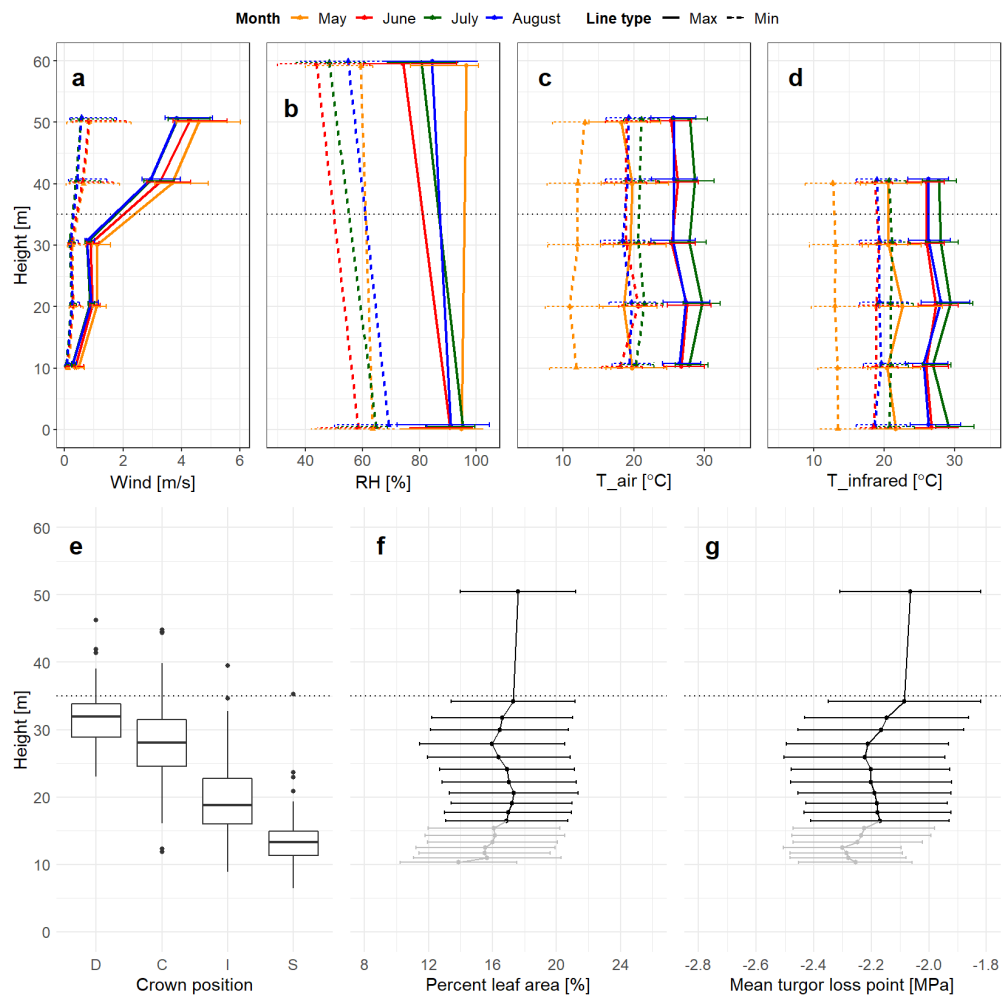Figure 2: Time series of combined tree cores by species

Figure 3: Height profile graphs

		Overall		1964		1977		1999	
variable_description	null_variables	dAICc	coefficients	dAICc	coefficients	dAICc	coefficients	dAICc	coefficients
drought.year	NA	35.834	1977 (-0.09), 1999 (-0.081)	NA	NA	NA	NA	NA	NA
ln[DBH]	Y	7.411	ln[DBH] (-0.035)	18.276	ln[DBH] (-0.082)	-0.947	ln[DBH] (-0.021)	-1.918	ln[DBH] (0.006)
ln[height]	Y	7.591	ln[H] (-0.058)	17.788	ln[H] (-0.133)	-1.077	ln[H] (-0.032)	-2.022	ln[H] (0.002)
crown.position alone	Y	-1.46	position_alldominant (-0.05	4.487	position_alldomina	0.15	position_alldom	0.444	position_alldominant (-0.011), p
crown.position w/height	ln[H]+Y	1.682	position_alldominant (-0.04	-2.548	position_alldomina	-0.7	position_alldom	4.087	position_alldominant (-0.003), p
ln[height]*ln[topographic.wetness.index]	ln[H]+ln[T]+Y	-2.018	ln[H]*ln[T] (-0.005)	0.035	ln[H]*ln[T] (-0.174)	-1.767	ln[H]*ln[T] (0.06	-1.785	ln[H]*ln[T] (0.057)
ln[topographic.wetness.index]	ln[H]+Y	2.88	ln[T] (-0.068)	-1.281	ln[T] (0.045)	4.728	ln[T] (-0.138)	2.621	ln[T] (-0.101)
ring.porosity	ln[H]+Y	-3.553	rpring (0.04), rpsemi-ring (0	-2.161	rpring (0.101), rpse	0.895	rpring (-0.19), rp	4.083	rpring (0.2), rpsemi-ring (0.151)
percent.loss.area	ln[H]+Y	4.413	PLA (-0.011)	5.825	PLA (-0.016)	-0.19	PLA (-0.01)	-0.701	PLA (-0.007)
leaf.mass.area	ln[H]+Y	-1.895	LMA (0.001)	-1.075	LMA (0.002)	-1.698	LMA (-0.001)	-1.985	LMA (0.0001)
mean.turgor.loss.point	ln[H]+Y	4.58	TLP (-0.207)	1.352	TLP (-0.217)	1.008	TLP (-0.236)	0.132	TLP (-0.177)
wood.density	ln[H]+Y	-2.018	WD (0.005)	-1.96	WD (-0.049)	-1.236	WD (-0.175)	0.171	WD (0.247)

#this is tested_traits_all

Results for third main question: are responses similar or variable across individual drought years? H3.1 and H3.2 Combining biophysical with hydraulic traits, which come out as candidates for best model?

Discussion

1. paragraph summarizing main results–> primary conclusions When including only biophysical traits, trees' resistance value (on a per-species basis) is explained best by crown position and height, with codominant trees being the most resistant to drought. This follows on work done by (Bennett et al., 2015) [and others?] which show that larger trees suffer more during drought, and confirms that this susceptibility can be seen in tree ring analyses. Adding in crown position with the leaf hydraulic traits yields a slightly worse predictive model for drought tolerance, with height remaining as the only significant biophysical variable.

We partially supported the hypothesis that crown exposure makes trees more vulnerable to drought. Co-dominant trees had the highest drought resistance. Dominant trees had lower resistance, likely because they are the most exposed. Other studies have found clear evidence of greater drought sensitivity in trees with exposed crowns (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)). At the same time, intermediate and suppressed trees had even lower resistance. This indicates that other mechanisms such as competition or rooting depth were important. (Also note that our study design was not ideal for testing the role of canopy position. Current canopy position is a conservative separator of canopy position: trees may currently be in more dominant positions than they were at the time, but backwards movement is unlikely. This would bias against finding a signficant effect for H1.2. Height may be a more reliable predictor of past canopy position than is current canopy position, and explains a portion of variation in canopy position.)

Proximity to stream–either vertical (elev) or horizontal (distance)– did not increase drought resistance; rather, it tended to decrease resistance (H1.3a). This may be because individuals growing further from water are acclimatized to drier conditions. However, the increase in drought resistance with distance from stream was less for small than large trees (H1.3b), indicating a potential importance of root depth/volume in conferring drought resistance.

misc content to integrate From (Kannenberg et al., 2019), species with diffuse porous wood anatomy (*Liriodendron*) are more sensitive to drought, whereas ring-porous are not as affected because they more easily rebuild structures for hydraulic conductivity. This paper mentions it would be good to have this data with respect to latent affects from drought. ### Conclusion

words

Supplementary Information

p50 and p80 We decided to include values of P50 and P80 in the leaf traits model, defined by (Anderegg et al., 2016) as the water potentials at which a species loses 50% and 88% [80% by proxy], respectively, of hydraulic conductivity. Values were calculated by (**insert new methods here??**), and were only available for six species (*C. glabra*, *L. tulipifera*, *Q. alba*, *Q. prinus*, *Q. rubra*, and *Q. velutina*). Because of this, the

Species-specific height regression equations

Species	Equations	r.2
Carya cordiformis	0.348+0.808*x	0.879
Carya glabra	0.681+0.704*x	0.855
Carya ovalis	0.621+0.722*x	0.916
Carya tomentosa	0.776+0.701*x	0.894
Fagus grandifolia	0.708+0.662*x	0.857
Liriodendron tulipifera	1.32+0.524*x	0.761
Quercus alba	1.14+0.548*x	0.647
Quercus prinus	0.44+0.751*x	0.869
Quercus rubra	1.17+0.533*x	0.773
all	0.879+0.634*x	0.857

model runs were considered to be incomplete due to the exclusion of the other 8 species. Results revealed neither p50 nor p80 to be significant, thus for the full analysis we decided to drop the two traits in order to include all species in the full analysis.

Candidate variables for best model

prediction	variable	variable_description	top_model
1.2	position_all	crown.position w/height	1999
2.2	height.ln.m	ln[height]	all
2.2	height.ln.m	ln[height]	1966
2.3	position_all	crown.position alone	1966
2.4	TWI.ln	ln[topographic.wetness.index]	all
2.4	TWI.ln	ln[topographic.wetness.index]	1977
2.4	TWI.ln	ln[topographic.wetness.index]	1999
3.1	year	drought.year	all
3.1	rp	ring.porosity	1999
3.2	PLA_dry_percent	percent.leaf.area	all
3.2	PLA_dry_percent	percent.leaf.area	1966
3.4	mean_TLP_Mpa	mean.turgor.loss.point	all

how do we want to present Table S3? Would it be better as an image of an excel file, since it's so large? Did we want to keep all coefficients here?

| variable_description	null_variables	Overall		1964		1977		1999	
		dAICc	coefficients	dAICc	coefficients	dAICc	coefficients	dAICc	coefficients
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#this is tested_traits_all (see Issue #32)
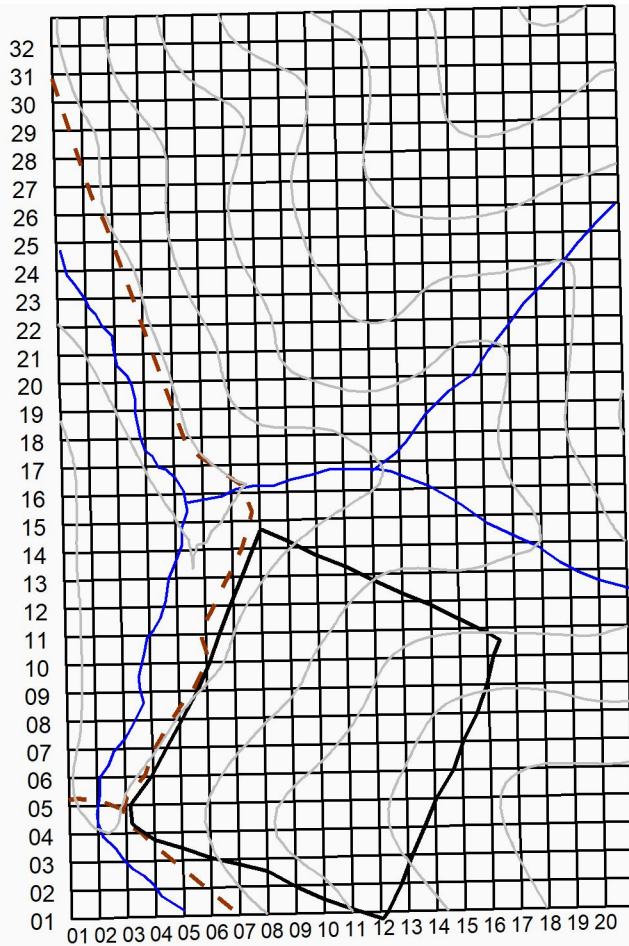
Figure 4: Map of ForestGEO plot

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Top model variations for each drought scenario, with dAICc values <= 2

Modnames	Delta_AICc
resist.value ~ position_all+height.ln.m+TWI.ln+year+PLA_dry_percent+mean_TLP_Mpa+(1|sp/tree)	0.00
resist.value ~ height.ln.m+TWI.ln+year+PLA_dry_percent+mean_TLP_Mpa+(1|sp/tree)	0.84
resist.value ~ position_all+height.ln.m+year+PLA_dry_percent+mean_TLP_Mpa+(1|sp/tree)	1.57
resist.value ~ height.ln.m+rp+PLA_dry_percent+(1|sp)	0.00
resist.value ~ height.ln.m+TWI.ln+rp+PLA_dry_percent+(1|sp)	1.37
resist.value ~ height.ln.m+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	1.39
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.00
resist.value ~ position_all+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.28
resist.value ~ height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	1.06
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+(1|sp)	0.00
resist.value ~ position_all+height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.05
resist.value ~ position_all+height.ln.m+TWI.ln+rp+(1|sp)	0.55
resist.value ~ position_all+height.ln.m+rp+mean_TLP_Mpa+(1|sp)	0.94
resist.value ~ TWI.ln+rp+PLA_dry_percent+(1|sp)	1.07
resist.value ~ position_all+height.ln.m+rp+PLA_dry_percent+(1|sp)	1.15
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1|sp)	1.41
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	1.82
resist.value ~ position_all+height.ln.m+rp+(1|sp)	1.88

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